ENVIRONMENTAL AND EVOLUTIONARY PROCESSES AFFECTING POPULATION DYNAMICS AND LIFE-HISTORY OF ARCTIC GRAYLING IN WESTERN AND INTERIOR ALASKA

By

Jenny Lou Neyme

RECOMMENDED:

Advisory Committee Co-Chair

Advisory Committee Co-Chair

Director, Fisheries Division

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

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ENVIRONMENTAL AND EVOLUTIONARY PROCESSES AFFECTING POPULATION DYNAMICS AND LIFE-HISTORY OF ARCTIC GRAYLING IN WESTERN AND INTERIOR ALASKA

A

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Jenny Lou Neyme, B.S.

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ABSTRACT

I compared the life-history and population dynamics of Arctic grayling *Thymallus arcticus* in Western and Interior Alaska. Fish in Western Alaska grew rapidly to a large maximum size, adult mortality rates were low and juvenile mortality rates were high. As a result, Western populations consisted mainly of larger, older fish. Fish in Interior streams grew more slowly to a smaller maximum size, adult mortality rates were higher and juvenile mortality rates lower than in Western streams. As a result, Interior populations consisted mainly of smaller, younger fish. The relationship between body size and ovary mass was similar between regions, but Interior fish allocated a greater proportion of their annual energy budget to reproduction.

I also used a foraging model to test the hypothesis that regional differences in drift-feeding opportunities were responsible for faster growth and larger size in Arctic grayling in Western Alaska and to determine the relative contribution of invertebrate drift density and physical habitat characteristics to regional differences in profitability. The model predicted that drift-feeding would be more profitable in Western Alaska and that regional differences in invertebrate drift density and size composition were responsible for this difference.

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GENERAL INTRODUCTION

Western and Interior Alaskan Arctic grayling *Thymallus arcticus* have distinctly different life-histories and population dynamics. Surprisingly, there has been little effort to synthesize and interpret information on this subject, though it is of considerable interest to fish ecologists and fishery managers.

My primary objective was to characterize the differences in life-history and population dynamics that exist and develop an understanding of the processes that might be responsible. To do this I compiled and analyzed data that have been collected over the years by biologists at the Alaska Department of Fish and Game, supplementing this work by collecting field data on the reproductive effort of fish in the two regions. This work is described in Chapter 1.

My second objective was to test the hypothesis that regional differences in drift-feeding opportunities were responsible for Arctic grayling in Western Alaskan streams growing more quickly and to a larger size than those in Interior Alaskan streams. I used the foraging model developed by Hughes et al. (2003) to predict the maximum net rate of energy intake for fish in each region and to determine the relative contribution of depth and velocity to predicted profitability. This work is described in Chapter 2.

In the general conclusions, I summarize the results of Chapters 1 and 2 and make recommendations for future research and management.

Chapter 1

A comparative analysis of the life-history and population dynamics of Arctic grayling in Western and Interior Alaska[a]

Abstract

I compared the life-history and population dynamics of Arctic grayling *Thymallus arcticus* in Western and Interior Alaska. Fish in Western Alaska grow rapidly to a large size, adult mortality rates are very low and juvenile mortality rates are high. As a result, Western populations consist mainly of larger, older fish. Fish in Interior streams grow more slowly to a smaller size, adult mortality rates are higher and juvenile mortality rates lower than in Western streams. As a result, Interior populations consist mainly of smaller, younger fish. The relationship between body size and ovary mass is similar between regions, but Interior fish allocate a greater proportion of their annual energy budget to reproduction. Fish densities in Interior streams are higher than in Western streams. These regional differences may be the result of high predation rates on juvenile fish in Western Alaskan streams which also have larger salmon runs and higher water temperatures. These factors may reduce competition for food, improve opportunities for growth, and favor the evolution of rapid growth and large size in Western streams.

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[a] Neyme, J.L. and N.F. Hughes. A comparative analysis of the life-history and population dynamics of Arctic grayling in Western and Interior Alaska. Transactions of the American Fisheries Society. In preparation.

Introduction

Fisheries biologists have long recognized that the life-history characteristics and population dynamics of Interior and Western Arctic grayling *Thymallus arcticus* are distinctly different (McCart and Pepper 1971; Armstrong 1986; Northcote 1995; Redenbach and Taylor 1999; Stamford 2001). Arctic grayling in Western Alaska grow faster and to larger sizes than Arctic grayling in Interior Alaska. They also have much lower adult mortality rates and, presumably, higher early life-history mortality. These patterns are consistent within regions and consistently different between regions.

The processes responsible for these regional differences are currently unknown, but may be the consequence of local adaptation of the life-history to regionally distinct ecological settings. Insights into the processes that might be responsible are provided by studies of life-history evolution in guppies *Poecilia reticulate*. Reznick and Endler (1982) describe life-history differences between populations of guppies that in many ways parallel the observed regional differences in Arctic grayling and attribute these differences to predator-mediated, age-specific survivorship. Similar age-specific differences in survival may underlie regional differences in the life-histories observed in Arctic grayling. Other ecological factors may also play a role in producing regional differences in life-history. For example, differences in per capita resource abundance or seasonal temperature regime may affect growth rates (Deegan et al. 1999; Dion

and Hughes 2004), and regional differences in the frequency and severity of floods may affect recruitment rates (Clark 1992).

Regional differences in the life-history and population dynamics of Arctic grayling are well known to fisheries biologists; however, data relating to this subject have never been fully analyzed or interpreted, nor has this subject been treated in the published literature. In this study, I compiled, analyzed, and interpreted available data relating to the life-history and population dynamics of Arctic grayling in four well studied Interior and Western Alaskan streams. I supplemented this information with field data on reproductive investment from one representative stream in each region. The objective of my analysis was to develop a coherent description of regional differences and propose how life-history evolution and other ecological processes may generate these differences.

Methods

Study Area

The rivers of study were all considered rapid runoff rivers (Reed 1964; Tack 1980) and are characterized by alternating pool and riffle habitats with long run sections. Arctic grayling overwintering, spawning, and feeding habitats were present in all study rivers. Western region study streams were represented by the Snake (64° 34' N, 165° 20' W) and Sinuk (64° 44' N, 165° 54' W) Rivers on the Seward Peninsula (Figure 1.1). The Snake and the Sinuk rivers are approximately 57 km and 75 km in length, respectively, with mean discharges of 7 m^3/s and 25 m^3/s when sampled. Western streams are considered part of the

"Transitional-continental climatic zone" where summer temperatures are moderated by oceanic influences and winter temperatures are similar to those of the Interior (Cushing et al. 1995). Average annual precipitation for the Nome area is 40.8 cm and the average annual temperature minimum and maximum are -6.89 ˚C and 0.78 ˚C respectively. Average total snowfall is 150.62 cm with an average snow depth of 15.24 cm (WRCC 2004).

Western vegetation is characterized as upland tundra and is dominated by grasses, sedges, and forbs (Cushing et al. 1995). Dwarf willows and small birches follow the riparian corridors (Cushing et al. 1995).

The fish communities for the Snake and Sinuk Rivers include: round whitefish *Prosopium cylindraceum*, Northern pike *Esox lucius*, slimy sculpin *Cottus cognatus*, Arctic char *Salvelinus alpinus*, Dolly Varden *Salvelinus malma*, burbot *Lota lota* and chinook *Oncorhynchus tshawytscha*, chum *O. keta*, sockeye *O. nerka*, coho *O. kisutch*, and pink *O. gorbuscha* salmon.

Interior region streams were represented by the Goodpaster River (64˚ 22' N, 144˚ 57' W) and the Chena River (64˚ 22' N, 146˚ 39' W) (Figure 1.2). The Chena River and the Goodpaster are approximately 260 km and 200 km in length, respectively. Mean annual discharge for the Chena and Goodpaster Rivers was 19.4 m^3/s and 12.5 m^3/s, respectively, (USGS 2005). The Interior is part of the "Continental" climate zone and is characterized by wide temperature regimes. Average annual precipitation for the Fairbanks area is 26.67 cm and the average annual temperature minimum and maximum are -8.33 ˚C and 2.72 ˚C,

respectively (Cushing et al. 1995). Average total snowfall is 170.92 cm with an average snow depth of 20.33 cm (WRCC 2004).

Interior sites are characterized by moderate-growth stands of boreal forest (Cushing et al. 1995). Typical vegetation in this region includes: white and black spruce *Picea glauca* and *P. mariana*, paper birch *Betula papyrifera*, *B. resinifera*, poplars *Populus trichocarpa* and *P. balsamifera*, quaking aspen *P. tremuloidies*, and the American larch *Larix laricina* (Cushing et al. 1995).

The fish communities found in the Goodpaster and Chena River include similar species as those found in Western Alaska, but are generally less diverse. Fish communities in the Chena and Goodpaster River include: chinook and chum salmon, humpback whitefish *Coregonus pidschian*, lamprey *Lamperta appendix* and large-nose suckers *Catostomus catostomus*, char *Salvelinus* species are not found.

Data Sources

Analyses were conducted using the following multi-year stream specific mark-recapture data sets unless otherwise stated.

Chena River

The Chena River analysis was based on data collected in the lower 140 km of the river by the Alaska Department of Fish and Game (ADF&G) for the period between 1987 and 1995 (R.A. Clark, ADF&G, unpublished). Sampling was conducted using a pulsed-DC electrofishing boat. Fish were measured for fork length (mm) and scales were collected for fish ≥ 150 mm in length. Fish were

tagged using Floy FD-67 internal anchor tags from 1987 to 1993. From 1987-1990, four 3.2 km sections were sampled in the lower 72 km as well as a larger section from km 72 to km 140. From 1991 to 1993, the entire 140 km section of the river was electrofished. This analysis was combined with hook and line sampling data collected by Hughes in 1992 to create a wholestream dataset (Hughes 1999). Hughes measured fork length (mm) for 683 fish sampled from the upper river (river km 140 to 240).

Goodpaster River

The Goodpaster River analysis was based on data collected by ADF&G for the period between 1995 and 1997 (W.P. Ridder, ADF&G, unpublished). Data were collected each year in May on the lower 96 km of the mainstem and North Fork of the Goodpaster. In 1996 and 1997, sampling was conducted in May and August but the area sampled was reduced to the lower 53 km of the river. All samples were collected using pulsed-DC electrofishing. All fish were measured (fork length mm) and tagged with Floy FD-67 internal anchor tags.

Snake River

The Snake River analysis was based on data collected by the ADF&G (A.L. DeCicco, ADF&G, unpublished) from 1991 to 1995. In 1991 fish were collected from a 28 km section of the river using a pulsed-DC electrofishing boat (DeCicco 1992). From 1992 onward the sample area was increased to 48 km of the river. In 1992 samples were collected using the electrofishing system and a 50-m × 2-m beach seine with 6.5-mm mesh (DeCicco 1992). From 1993 to 1995

only seining was used in sample collection (DeCicco 1994, 1995, 1996). All sampled fish were measured for fork length, tagged with Floy FD-67 internal anchor tags and scales were collected (DeCicco 1992, 1993, 1994, 1995, 1996).

Sinuk River

The Sinuk River analysis was based on data collected by the ADF&G (A.L. DeCicco, ADF&G, unpublished) over a 40 km section of river from 1989 to 1993. From 1989-1992 samples were collected using hook and line (DeCicco 1990, 1991, 1992, 1993, 1994). In 1993 the samples were collected using a 50-m × 2-m beach seine with 6.5-mm mesh (DeCicco 1994). Sampled fish were measured for fork length, and tagged with Floy FD-67 internal anchor tags and scales were collected (DeCicco 1990, 1991, 1992, 1993, 1994).

Growth Rates

To compare growth rates of Western and Interior Arctic grayling, I fit von Bertalanffy growth curves using mark-recapture data from the four study streams following Ricker (1975). Multiple years of data were combined to create a larger data set represented by: Chena 1986-1993 n=1,148, Goodpaster 1995-1997 n=132, Snake 1992-1995 n=213, and Sinuk 1991-1992 n=93. I seeded the Walford line using mean length at age 3 from scale-based ages for the Chena (214 mm, 95% CI ± 3 mm, n=110); Goodpaster (199 mm, 95% CI ± 2 mm, n=156); Snake (261 mm, 95% C I± 10 mm, n=29); and Sinuk Rivers (271 mm, 95% CI ± 11 mm, n=2). Ninety-five percent confidence intervals were calculated using (n=1,000) bootstrap replicates (Quinn and Deriso 1999).

Population Structure

To describe differences in the size structure of Interior and Western populations, I compared length-frequency distributions from the four study streams. For the Chena River I obtained data from previous mark-recapture experiments (Tack 1974; Hughes 1999; R.A. Clark, ADF&G, unpublished; A.L. DeCicco, ADF&G, unpublished). Year of sampling and sample sizes are as follows: Chena 1992: n=6,289, Goodpaster 1995 n=1,287, Snake 1995: n=380 and Sinuk 1997: n=128.

Density and Abundance

To determine fish densities in Interior and Western streams, I combined published estimates of fish abundance per km of river length with estimates of mean stream width in the assessed reach. For the Chena River I used data from Wuttig (2004) for a 20 km section of the upper river in 2002 and Tack (1974) for the upper 87 km of the Goodpaster in 1973. Western density estimates for 1992 were taken from DeCicco (1994) for a 48 km stretch of the Snake River and 40 km of the Sinuk River.

To estimate stream width, I averaged four representative width measurements on each stream, at high and low flows. I calculated fish per m^2 for each stream by dividing fish per meter density estimates by mean width.

Abundance information was synthesized from existing reports (Clark 1993; DeCicco 1994; Ridder 1998; Gryska 2004).

Reproductive Investment

To compare reproductive investment of female Arctic grayling in Interior and Western regions, I collected data on the proportions of spawners vs. nonspawners among potentially mature fish, ovary mass, fecundity, egg size, and age at maturity. I also estimated mean fecundity for each population.

I sampled fish from one river in each region, the Chena River in Interior Alaska and the Snake River in Western Alaska. For the Chena River my analysis was based on a sample of 13 adult females larger than 210 mm, the length at which 50% of fish are mature, (Clark 1992). Fish were captured with an electrofishing boat at the beginning of the spawning period in May of 2004. On the Snake River, I sampled 8 female fish larger than 300 mm, the length at which 50% are mature (Gryska 2004). Fish were sampled using hook and line and a gillnet. All fish were measured to the nearest millimeter (fork length), weighed to the nearest 0.1g using an electronic balance (Acculab V-333) and frozen for transport to the lab.

In the lab, I examined the state of egg development to determine the proportion of spawning fish in each sample. Fish with large (>2.0 mm) well developed eggs were considered likely to spawn that year (de Bruyn and McCart 1974), while fish with eggs smaller than 0.5 mm were considered unlikely to spawn that year.

To determine ovary mass, I weighed ovaries to the nearest 0.01g on an electronic balance (Ohaus CS-2000). To determine fecundity and egg size, I used methods described in Skaugstad and McCracken (1991).

I obtained Information on age at maturity in the Chena, Goodpaster, and Snake Rivers from published sources (Clark 1992; Gryska 2004).

I estimated mean female fecundity in each of the four populations by combining information on length at maturity, the relationship between fish size, and fecundity, and the length-frequency distributions I used to describe population size structure.

Survival and Recruitment

I obtained estimates of annual survival for Arctic grayling in the Chena from Clark (1996). Clark provides a Jolly-Seber estimate of survival of fish larger than 175 mm in the lower 152 km of the river between 1994 and 1995. To estimate annual survival for fish in the Goodpaster River, I performed Jolly-Seber estimates (Ricker 1975) using data from a four year mark-recapture experiment described by Parker (2002). This allowed me to estimate annual survival of fish larger than 270 mm in the lower 53 km of the river for the years 1995-96, 96-97, and 97-98 and I used the geometric mean of these estimates as the best estimate of annual survival. To estimate annual survival in the Snake and Sinuk Rivers I performed Jolly-Seber estimates using unpublished ADF&G data for five year mark recapture experiments (Snake 91-95 and Sinuk 89-93) using the geometric mean as the best estimate of annual survival.

To determine whether there are marked regional differences in early life-history mortality, I estimated egg-to-adult survival by dividing the annual mortality rate of mature fish (1-Survival rate) by mean adult fecundity (mean female fecundity × 0.5). By analyzing this statistic, in conjunction with estimates of adult survival rates, it should be possible to detect regional differences in mortality rate during the first two years of life.

Results

Growth Rates

The von Bertalanffy growth curves show that growth patterns of Western and Interior fish are distinctly different (Figures 1.3, Table 1.1). Western Alaskan fish grow more quickly than Interior fish and to a larger size. Scale-based ages show that at age 3 Western Alaskan fish already averaged 60 mm longer than Interior fish (199 ± 2 mm and 214 ± 3 mm vs. 261 ± 10 mm and 271 ± 11mm), showing that Western Alaskan fish grow more quickly than Interior Alaskan fish in early life. Older Western fish continue to grow more rapidly than Interior fish and the growth analysis predicts that by age 15 Western Alaskan fish will, on average, be approximately 90 mm longer than Interior fish.

Population Structure

The length-frequency analysis demonstrates that the size structure of Arctic grayling populations in Interior and Western Alaska are distinctly different (Figure 1.4). Small fish are numerically dominant in Interior populations, while large fish are numerically dominant in Western populations. This difference in

size structure is so marked that fish in the 150-300 mm size range, which are numerically dominant in Interior populations, are practically absent in Western populations; while fish in the 350-500 mm size range, which are numerically dominant in Western populations, are relatively uncommon in Interior populations. Mean modal lengths were 227.5 mm and 426 mm for Interior and Western populations, respectively. This length-frequency analysis shows that Interior populations are numerically dominated by young fish, with older fish being progressively less abundant; whereas, Western populations are numerically dominated by older fish.

Density and Abundance

Density of fish in Interior streams was higher than in Western streams. The Chena and Goodpaster rivers held densities of 0.0021 fish/m^2 and 0.0017 fish/m^2 (mean=0.0019 fish/m^2), respectively. While the Snake and Sinuk Rivers had much lower estimated densities of 0.0015 fish/m^2 and 0.0008 fish/m^2 (mean= 0.0011 fish/m^2), respectively.

Abundance estimates were correspondingly higher for Interior streams: Chena 26,756 fish 95% CI ± 6,441 (Clark 1993), Goodpaster 23,194 fish 95% CI ± 4,392 (Ridder 1998). Estimates for Western streams were as follows: Snake River 1,761 fish 95% CI ± 253 (DeCicco 1994) and Sinuk River 1,782 fish 95% CI ± 500 (DeCicco 1994).

Reproductive Investment

Seven (54%) of the fish sampled from the Chena River had large, well developed eggs and were ready to spawn that season, the remaining 6 (46%) fish had small, undeveloped eggs and were considered unlikely to spawn that season. Two (25%) of the fish sampled from the Snake River were ready to spawn that season, the remaining 6 (75%) were considered nonspawners. The nonspawners spanned the full size range sampled and in the Chena River included fish of: 250, 270, 342, 350, and 390 mm and in the Snake included fish of: 300, 342, 344, 350, and 388 mm fork length. It seems unlikely that fish of this size were immature and this raises the possibility that Arctic grayling do not spawn every year, as previously believed.

Although sample sizes were small, there is little suggestion that the relationship between fish length or fish mass and ovary mass of prespawning fish differs between populations in the Snake and Chena rivers (Figures 1.5, 1.6). The gonadosomatic index (ovary mass/fish mass) increased from 0.14 for a 250 mm fish to 0.19 for a 500 mm fish.

Both fecundity and egg size increased with fish size. There was no indication that the relationship between fish size and fecundity or fish size and egg size differed between the Chena and Snake River (Figures 1.7,1.8). Estimated mean fecundity of fish in Western Alaskan populations was significantly higher than in Interior populations (Table 1.2).

Fish in the Snake and Goodpaster Rivers were reported to mature at age 6 (Clark 1992; Gryska 2004), while Chena River Arctic grayling have been documented as maturing two years earlier at age 4 (Clark 1992). No information on Sinuk fish is available.

Taken as a whole these results suggest that there is no dramatic difference in the relationship in energy allocation and fish size between regions. However, as a consequence of their larger size, mature fish in Western Alaska are considerably more fecund and spawn larger eggs than their counterparts in Interior Alaska.

Survival and Recruitment

Annual survival of adults in Western Alaska was much higher than for Interior fish (Table 1.2). Mean survival estimates were 1.0 ± 0.19 for Western fish and 0.62 ± 0.07 for Interior fish. Regional differences in egg-to-adult survival followed the opposite pattern (Table 1.2), with mean survival rates in Interior populations approximately 5-10 times higher than in Western populations.

Discussion

My analyses showed that there are distinct regional differences in life-history and population dynamics of Arctic grayling. Fish in Western Alaska grow more quickly throughout life and reach a larger maximum body size. Western populations are composed almost entirely of large (>300 mm) mature fish, while most fish in Interior populations are smaller than 300 mm.

Sample sizes were small, but there is no marked regional difference in the relationship between body size and the reproductive effort of spawning females or the relationship between body size and fecundity or egg size. This might suggest that reproductive investment is similar between regions, but the higher growth rate of Western fish means they probably allocate a smaller proportion of their annual energy budget to reproduction. These estimates of energy allocation are complicated by my discovery that Arctic grayling may not spawn annually, as previously believed (Armstrong 1986; Northcote 1995).

Annual mortality of mature Western fish were much lower than for Interior fish, but juvenile mortality was, correspondingly, much higher. Balancing these regional differences in mortality, the recruitment of mature fish in Western populations was much lower than in Interior populations.

These regional differences in patterns of growth, mortality, and recruitment explain regional differences in the size structure of Western and Interior populations. Difficulty in aging fish from scales prevented me from performing a detailed analysis of regional differences in age structure, but observed mortality and recruitment rates mean that Western populations must be dominated by considerably older fish than Interior populations. This inference is supported by the fact that the maximum validated age for a Western Alaskan grayling is 29 years (A.L. DeCicco, ADF&G, unpublished), while the maximum validated age for an Interior fish is only 11 (Merritt and Fleming 1991). These estimates are based

on small sample sizes of otolith-aged fish and further work is likely to increase the maximum known age, particularly in Western Alaska.

The regional differences in life-history of Arctic grayling parallel spatial variations in the life-histories described for guppies by Reznick and Endler (1982) and for brook trout *Salvelinus fontinalis* by Hutchings (1993). The work on guppies suggests that predator-mediated differences in age-specific mortality generate regional differences in life-history. When the mortality of large fish is high, relative to small fish, natural selection favors the evolution of early reproduction, high reproductive effort, high fecundity and small offspring. As a consequence of the trade-off between energy allocation to growth and reproduction, fish grow slowly and to a smaller maximum size. Conversely, when the mortality of small fish is high, relative to large fish, natural selection favors the evolution of delayed reproduction, low fecundity, large offspring, faster growth, and large maximum size. These two suites of life-history characteristics are very similar to the ones I observed for Western and Interior Arctic grayling, the only inconsistency being that I did not find regional differences in the total reproductive effort of spawning females, size-based fecundity or egg size. However, the slower growth of Interior fish does mean they allocate a greater proportion of their annual energy budget to reproduction.

The work on guppies suggests that regional differences in Arctic grayling life-history could be the result of high predation rates on small fish in Western Alaska, or high predation rates on large fish in the Interior. In light of this

prediction it may be significant that Western streams are frequented by large numbers of anadromous Dolly Varden, which undoubtedly prey on juvenile Arctic grayling. There is no comparable predator in the Interior and it is possible that Dolly Varden predation on young Arctic grayling in Western Alaska generates regional differences in life-history. Regional differences in the abundance of predators capable of consuming large Arctic grayling are not as obvious, but may exist. For example, burbot, a predator capable of consuming large prey, are present in both regions but are much less abundant in Western Alaska. High angler harvest rates of relatively large fish in the Chena River are thought to have selected for the early maturity observed in this population, and as a consequence, may reduce growth rate and maximum body size. If so, then this demonstrates that high adult mortality rates can result in life-history evolution.

So far, I have focused on the way regional differences in mortality rates might generate regional differences in life-history. However, differences in per-capita food abundance and seasonal temperature regime may also be important as both these factors can influence growth rate. Per-capita food abundance is probably highest in Western Alaska because large salmon runs boost food production and densities of Arctic grayling are relatively low, perhaps as a result of high predation rates on juvenile fish. Western Alaskan streams are also somewhat warmer than Interior streams (J.L. Neyme, University of Alaska Fairbanks, unpublished) and it is possible that the greater food abundance and warmer temperatures in Western Alaska combine to produce the fast growth and

large size of Western fish. If true, this suggests that higher temperatures do not necessarily depress the growth rate of large Arctic grayling as described by Deegan et al. (1999). Per-capita food abundance in the Arctic streams they describe is probably much lower than in Western Alaska and this will reduce the optimum temperature for growth.

Interestingly, growth opportunity may interact with predator-induced, size-dependent mortality rates to affect the evolution of growth rates. For example, Chase (1999) suggests that high growth rates will evolve when predation rates on small fish are high but opportunities for growth are sufficient for them to outgrow their predators. This process may contribute to the fast growth and large body size observed in Western Alaska. Recent work has shown that growth rate can evolve in response to size-dependent mortality rates (Conover and Munch 2002).

This study documents regional differences in life-history and proposes processes that may generate the observed patterns. However, a more complete understanding of patterns and processes would be valuable. Further work on age-specific mortality rates, causes of mortality, age structure, reproductive investment, growth, and the relative importance of environmental and genetic factors would be particularly useful.

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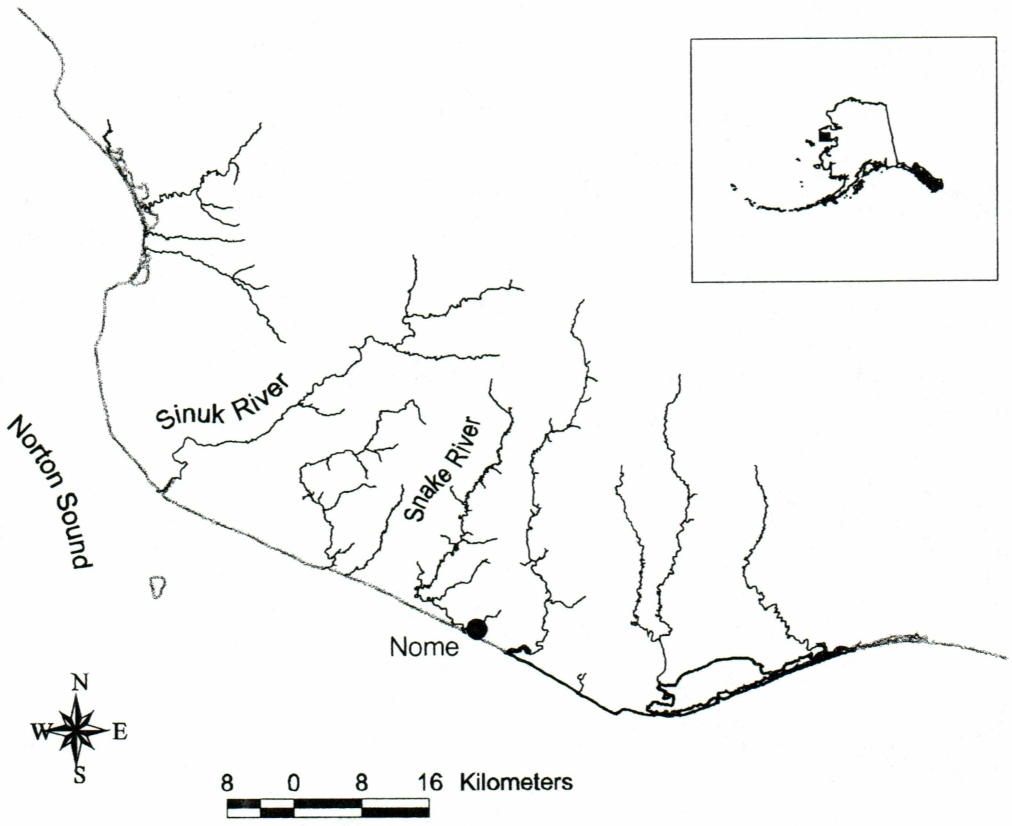


Figure 1.1-Map of the Snake and Sinuk Rivers in the Western region study area on the Seward Peninsula.

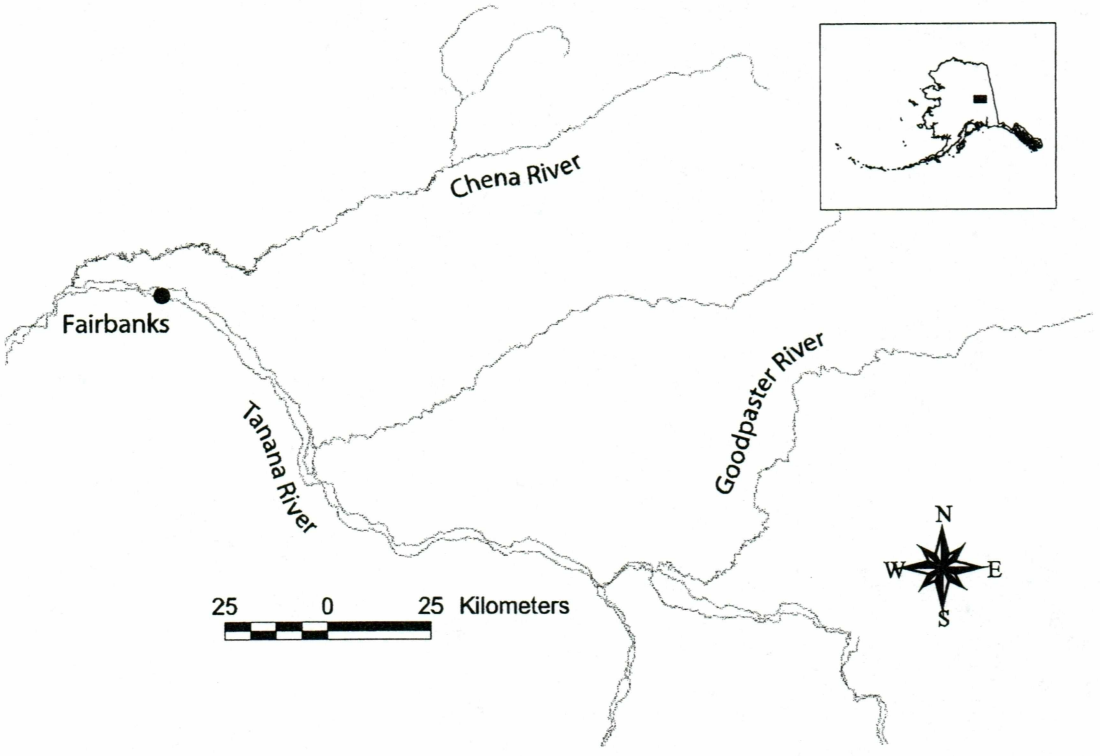


Figure 1.2-Map of the Chena and Goodpaster Rivers in the Interior region study area.

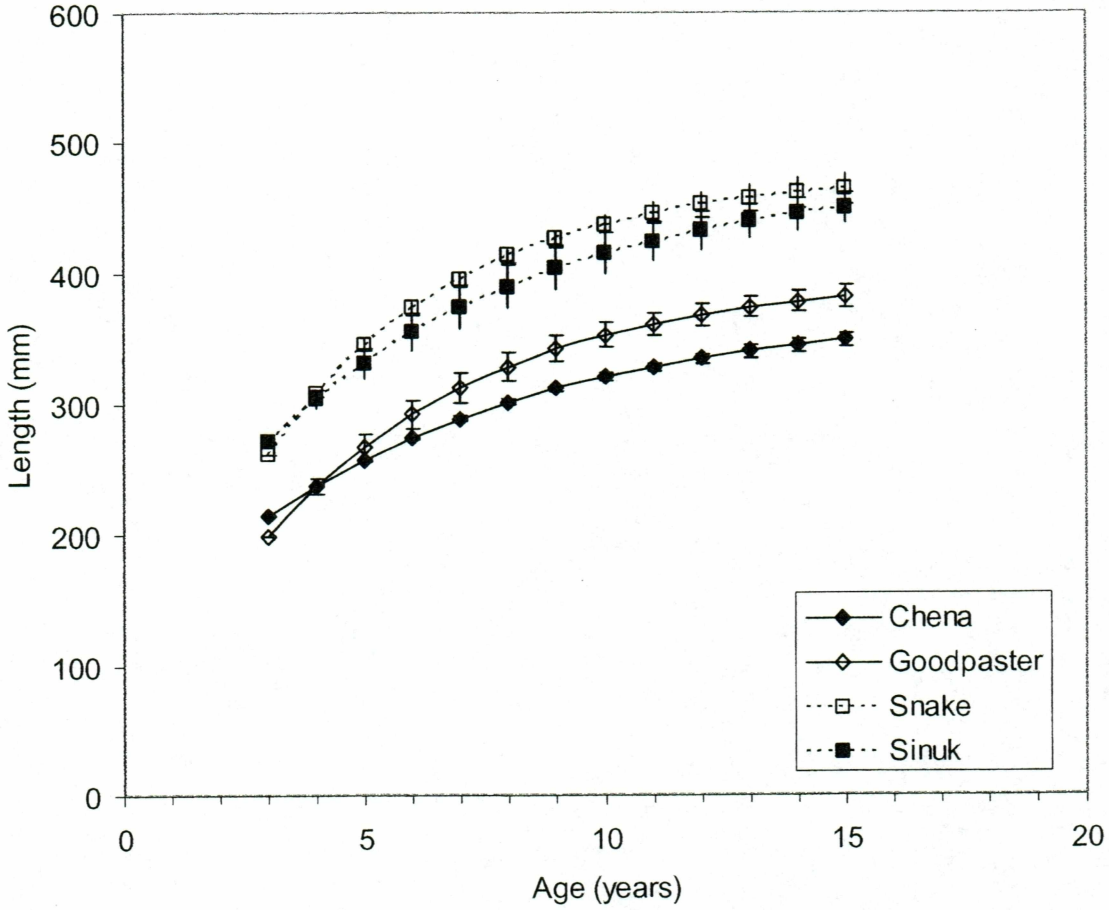
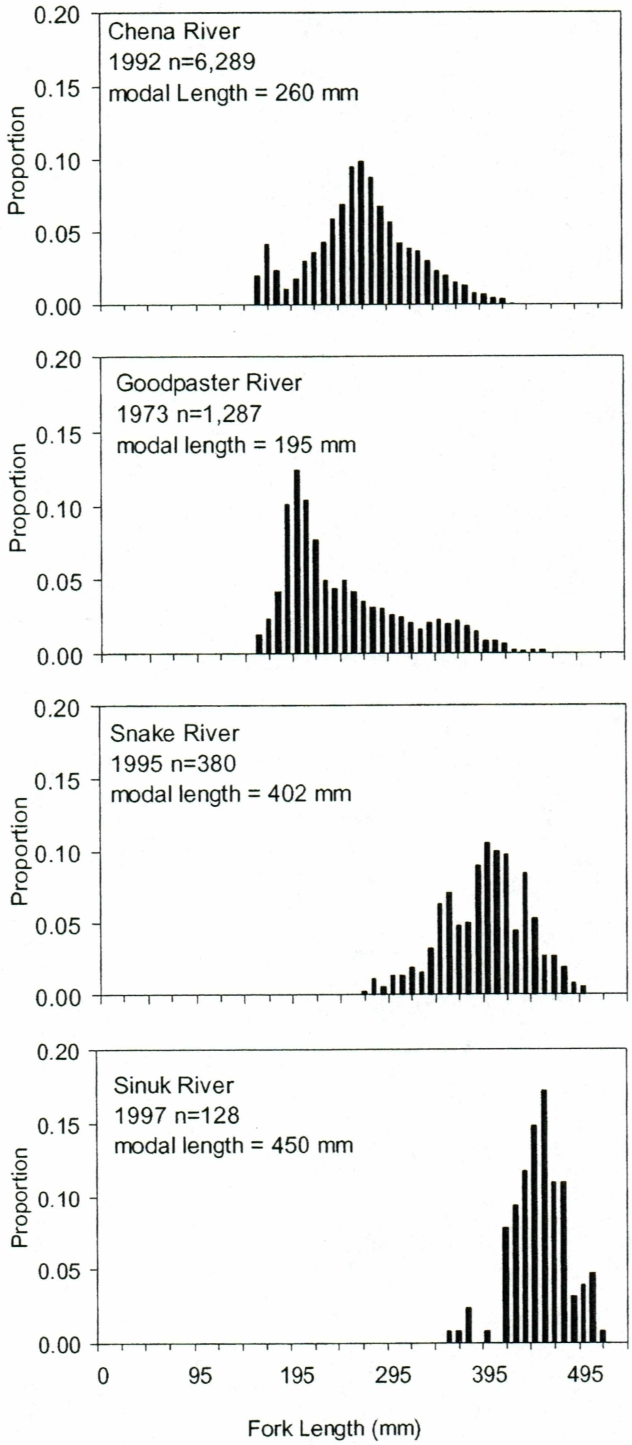


Figure 1.3-Mark recapture-based von Bertalanffy growth curves for Arctic grayling in the four study streams with 95% CIs on mean length at age.

Table1.1-Estimated von Bertalanffy growth parameters for the four study streams based on mark-recapture data, with 95% CIs.

	Chena	Goodpaster	Snake	Sinuk
L_∞ (mm)	372±10.03	400±15.93	475±17.90	474±12.89
K (1/t)	0.16±0.01	0.21±0.05	0.25±0.04	0.18±0.05
t_0 (years)	2.30±0.29	0.30±0.65	-0.56±0.26	1.76±1.19



Figures 1.4-Length-frequency distributions for fish sampled from the four study streams.

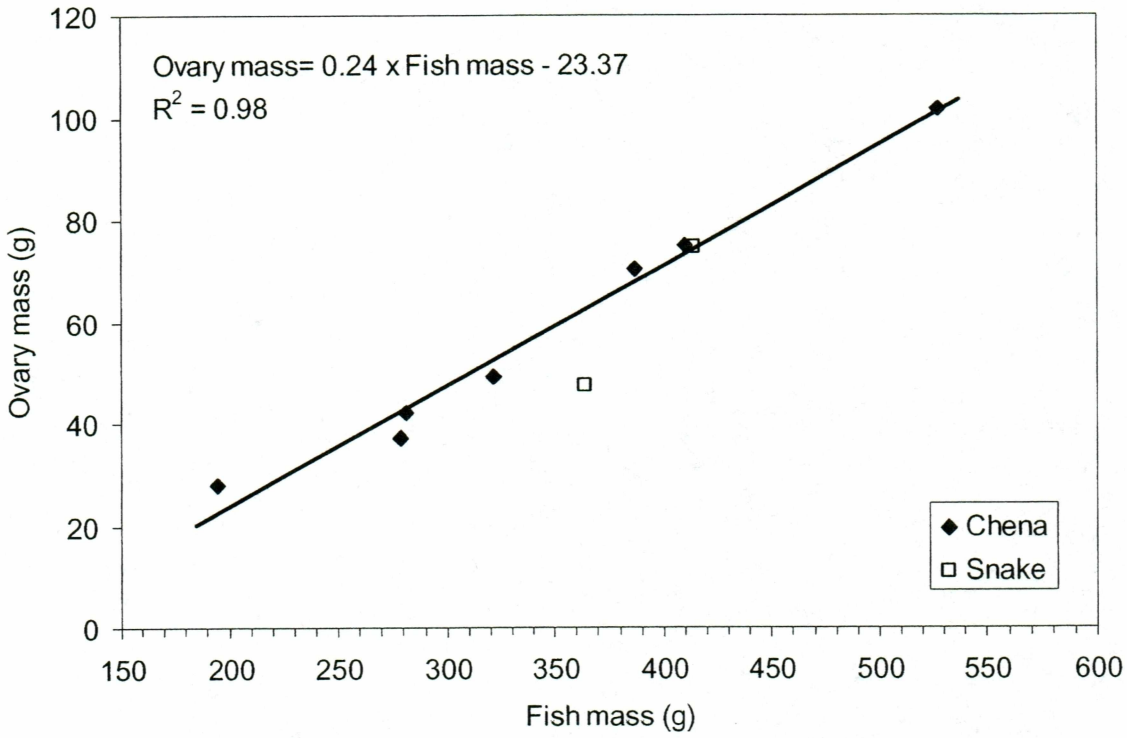


Figure 1.5-Regression of ovary mass on fish mass for Chena River fish with data for two Snake River fish shown for comparison.

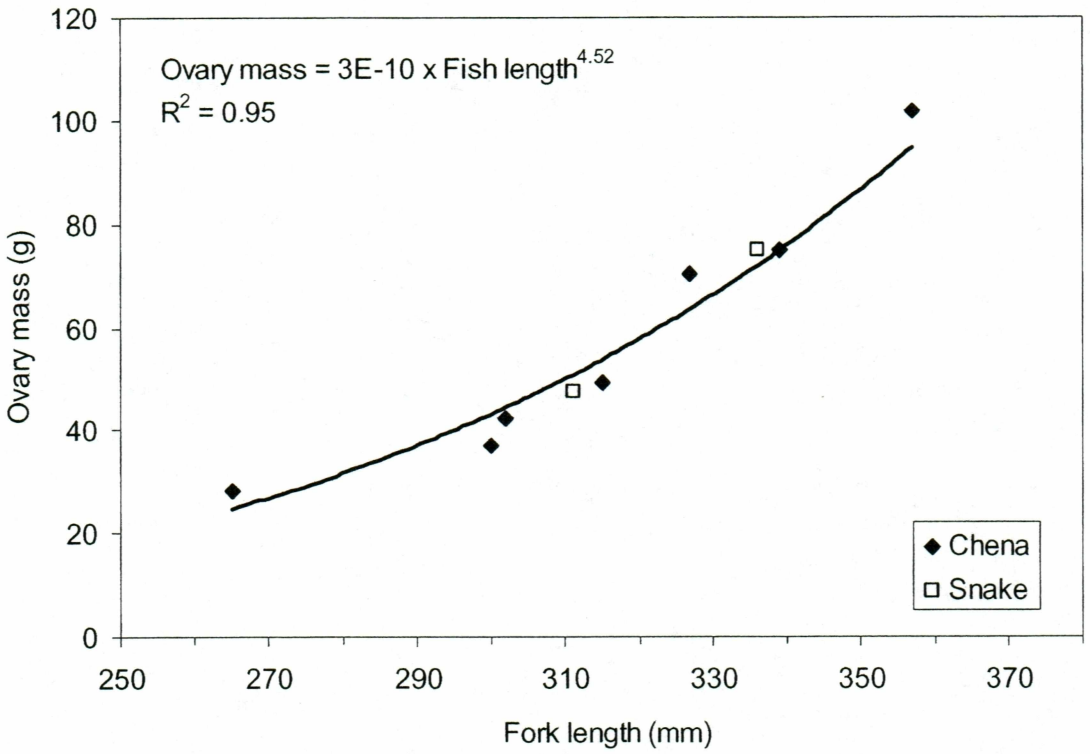


Figure 1.6-Ovary mass (g) as a function of fish length for sampled fish in the Chena (n=7) and Snake (n=2) Rivers with a power curve fitted to Chena data.

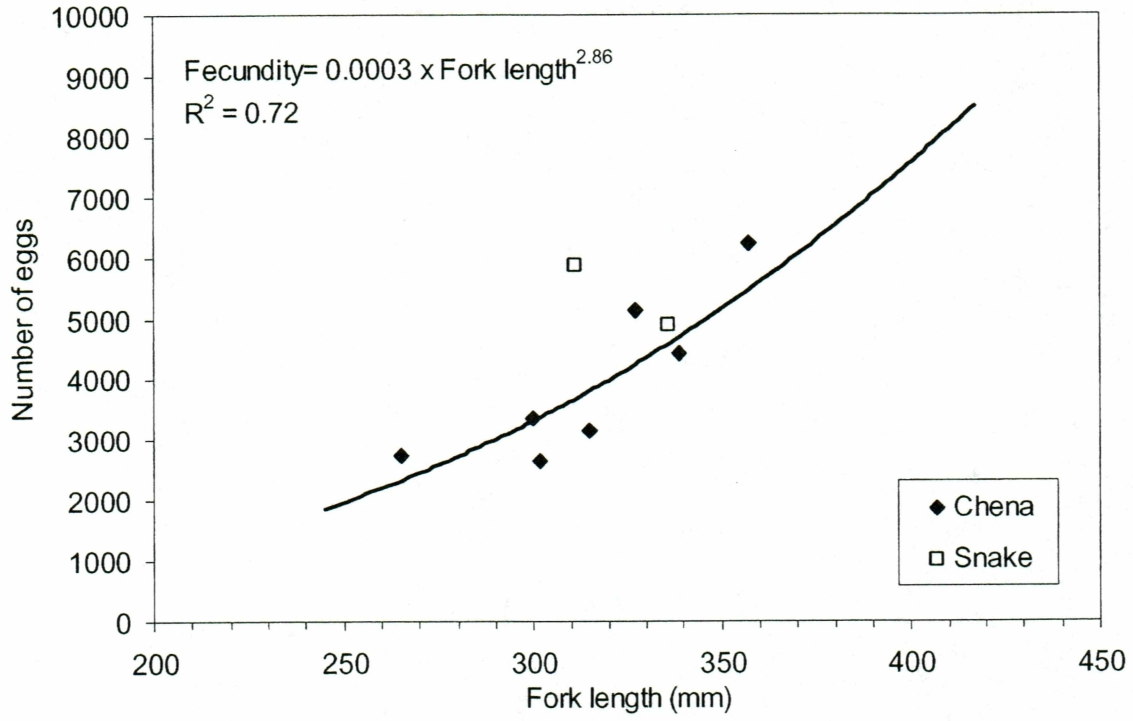


Figure 1.7-Fecundity (number of eggs per fish) as a function of fork length (mm) for fish sampled in 2004 from the Chena (n=7) and Snake (n=2) Rivers with a power curve fitted to Chena data. No significant difference between regional fecundity (F=5.32, p-value=0.05) was found.

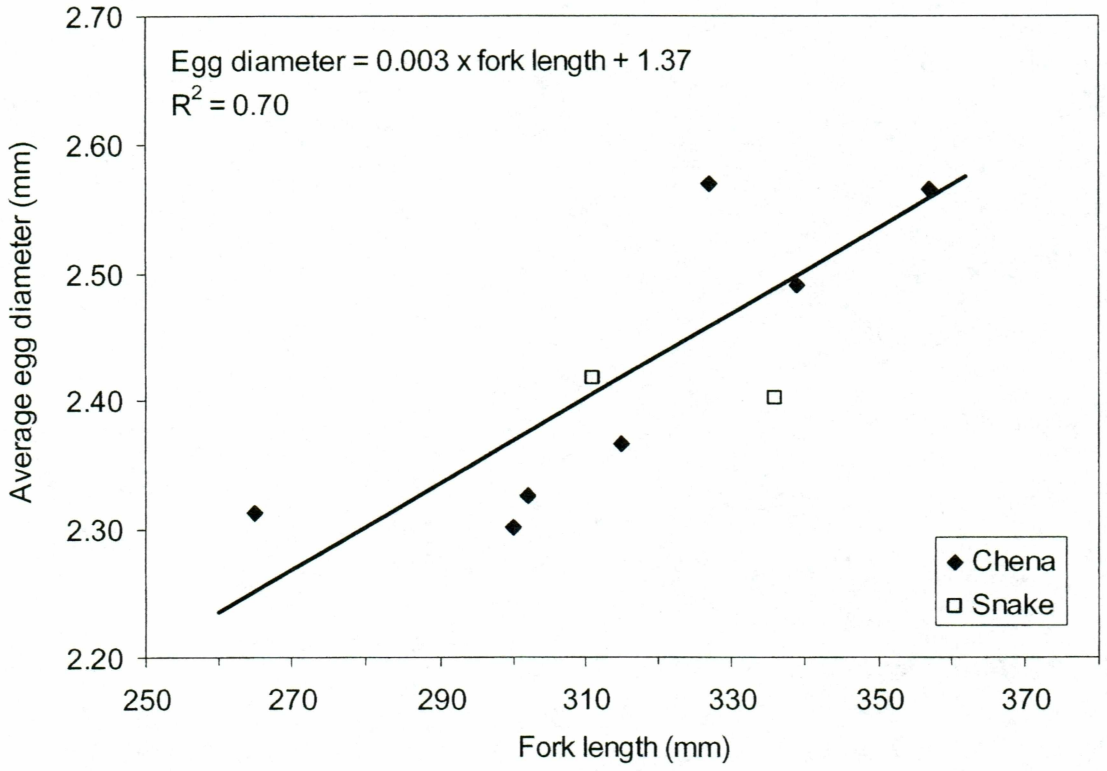


Figure 1.8-Average egg diameter (mm) as a function of fish length (mm) for fish sampled from the Chena (n=7) and Snake (n=2) rivers with linear regression line fitted to Chena data.

Table 1.2-Estimated annual survival and mortality rates for Arctic grayling larger than 150 mm in the four study streams with 95% CIs. Also, estimated mean fecundity, and egg to adult survival probability. Mean fecundity is 0.5 x the average female fecundity.

	Annual Survival	**Annual Mortality**	**Mean Fecundity**	**Egg to Adult Survival Probability**
Chena	0.63 ± 0.11	0.37	4,289	0.00008
Goodpaster	0.60 ± 0.09	0.40	2,781	0.00020
Mean Interior	0.62 ± 0.07	0.38	3,535	0.00014
Snake	0.92 ± 0.25	0.08	6,814	0.00003
Sinuk	1.08 ± 0.27	-0.08	8,991	0.00000
Mean Western	1.00 ± 0.19	0.00	7,902	0.00002

CHAPTER 2

Can regional differences in the profitability of drift-feeding explain regional differences in growth rate and maximum size of Arctic grayling?[a]

Abstract

I tested the hypothesis that regional differences in drift-feeding opportunities are responsible for Arctic grayling *Thymallus arcticus* in Western Alaskan streams growing more quickly and to a larger size than those in Interior Alaskan streams. I used a foraging model to predict the net rate of energy intake for fish feeding in two streams in each region on each of two dates, early and late summer. I also used the model to determine the relative contribution of invertebrate drift density and physical habitat characteristics to regional differences in profitability. The model predicted that drift-feeding would be more profitable in Western Alaska and that regional differences in invertebrate drift density and size composition are responsible for this difference. Most studies of habitat quality for drift-feeding fish focus on physical habitat characteristics, such as water depth and velocity, and devote little or no attention to invertebrate drift. This study suggests that it may be worthwhile to devote more attention to food availability in the future.

Introduction

[a] Neyme, J.L. and Hughes, N.F. Can regional differences in the profitability of drift-feeding explain regional differences in growth rate and maximum size of Arctic grayling? Transactions of the American Fisheries Society. In preparation.

Arctic grayling populations in Western Alaska grow more quickly and to a larger size than those in Interior Alaska (Chapter 1). The processes responsible for these regional differences are not understood, but might be the result of regional differences in life-history evolution, the interaction of seasonal temperature regime and per capita resource abundance (Chapter 1), or regional differences in the physical characteristics of the foraging habitat.

Experimental evidence has shown that growth rates and maximum size are life-history characteristics that can evolve as adaptations to the prevailing age-specific mortality rates (Reznick and Endler 1982; Conover and Munch 2002).

Elliott (1982) has shown that the most important environmental characteristics affecting growth are water temperature and food intake. As predicted by Elliott's work, a reduction in temperature has been shown to increase the growth rate of adult Arctic grayling in resource-poor streams (Deegan et al. 1999). In cool resource-rich streams an increase in temperature can be expected to increase growth rate. A reduction in per-capita food availability due to either increased density or decreased food input has also been shown to decrease growth rate (Keeley 2001). Deegan et al. (1999) found that high flows are correlated with an increase in adult Arctic grayling growth rates raising the possibility that the increase in depth and velocity associated with high flows may contribute to higher growth rates, but it is also possible that this

correlation is due to an association between high flow, drift density, and temperature.

In this study I used a foraging model (Hughes et al. 2003) to test the hypothesis that regional differences in foraging opportunity between Western and Interior Alaskan streams are responsible for regional differences in growth and maximum size. Arctic grayling are thought to feed primarily on invertebrate drift (Reed 1964; Vascotto 1970; Armstrong 1986) and adult Arctic grayling are known to establish dominance hierarchies and select the most profitable position that their dominance rank allows (Vascotto 1970; Hughes 1992a, b). In this situation, the energy intake of dominant fish should not be influenced by the abundance of subordinates and it is appropriate to use models of drift-feeding to predict their energy intake. This class of foraging model has been used to predict how physical characteristics such as depth and flow combine with invertebrate drift density to predict net rate of energy intake, growth, and position choice (Hughes and Dill 1990; Guensch et al. 2001; Hayes et al. 2003), but their ability to predict regional differences in growth rates has not yet been tested.

Methods

To test the hypothesis that the profitability of drift feeding is greater in Western Alaskan streams, I used the foraging model described by Hughes et al. (2003) and Hayes et al. (2003). I estimated the maximum net rate of energy intake (NREI) available to fish in two pools in each of two streams from each region on each of two occasions, once during early summer (June16-July 3,

2003) and once during late summer (August 13-28, 2003). I combined values from each sample period to estimate means for each stream and then calculated the two regional means. I tested the hypothesis that drift-feeding is more profitable in Western streams with a one-tailed *t*-test.

The Sinuk and Snake Rivers were chosen to represent Western Alaskan streams and the Chena and Goodpaster Rivers were chosen to represent Interior streams. Each pool sampled was selected because it was known to support large fish. These streams are described in more detail in Chapter 1.

The model described by Hughes et al. (2003) and Hayes et al. (2003) requires information on spatial variation in water depth and velocity in the modeled reach. I predicted this using a 2D flow model, River_2D (Steffler 1998). I used a Topcon GTS 600 series total station to survey bathymetry and bank topography for each of the four pools and also collected information on bed roughness (height of dominant roughness elements in meters) and downstream water surface elevation and discharge. To measure discharge I used a Marsh-McBirney Flowmate model 2000 flow meter. Bed roughness was similar in all pools corresponding to small cobble with a roughness height of 0.15 m. This information was converted into predictions of spatial variation of depth and velocity by River_2D (Figure 2.1).

Output from the flow model was prepared for input into the foraging model using two further computer programs. First it was fed into the streamlines program (Hayes et al. 2003), which divides the pool into a series of flow tubes

and cross-sections. Next output from the streamlines program was fed into the drift program (Hayes et al. 2003), which maps predictions of spatial variation in invertebrate drift density onto the flow tube based description and outputs a file containing the information on spatial variation in depth, velocity, and invertebrate drift density. The drift model is initialized with information on length-specific drift density at the upstream end of each modeled reach.

To obtain the necessary information on invertebrate drift, I collected samples during mid-afternoon during the early and late summer periods. Each sample was collected by fishing three drift nets for 20 minutes in the riffle upstream of each study pool. Nets were completely submerged and so collected only subsurface drift. The mouth area of each net was 0.139 m^2 and the mesh size was 360 microns. I used a Marsh-McBirney Flowmate model 2000 flow meter to measure water velocity at three locations spread across the mouth of each net and used this information to calculate the volume of water filtered. I stored invertebrate samples in Strex fixative. Later, in the lab, I sorted the samples, identified invertebrates to order, and classified individuals into 2 mm length categories. For each combination of taxon and length I estimated dry weight using relationships provided by Smock (1980) for aquatic insects and by Rogers et al. (1976) for terrestrial insects, and energy content using equations provided by Hughes (1992a). Finally, I estimated taxon and length-class specific drift density by dividing the number of individuals in each sample by the volume

of water filtered, I then averaged results to calculate pool means and stream means for each date.

To predict the maximum NREI available in each pool on each date I ran the simulations necessary to create maps of NREI and then selected the maximum predicted value for each pool and date combination (Figure 2.2). All simulations were run using the physical habitat and drift data from the appropriate dates. I used a representative fish with a length of 350 mm and a weight of 650 g, water temperature was set to 12 °C.

The analysis I have just described is designed to determine whether there are regional differences in foraging opportunities, but it will not distinguish the relative importance of regional differences in invertebrate drift density from regional differences in physical habitat. To determine whether regional differences in physical habitat characteristics were important, I also ran simulations for all pools and dates using a constant drift density (0.96 individuals/m^2) and size composition (5 mm). These values were representative of the invertebrate drift in the Chena and Sinuk River during early summer.

Results

My predictions suggest that Western Alaskan streams are significantly more profitable than Interior streams (P_{∞}= 0.028, Figure 2.3). The predicted regional mean for maximal NREI in Western Alaskan streams was 1.27 J/s compared to only 0.17 J/s in Interior streams. This difference was significant despite considerable between-stream and between-date variations in predicted

NREI (Figure 2.4). Between-date variation was not consistent within region, for example, predicted profitability for the Snake was highest in late summer whereas on the Sinuk it was highest in early summer. Another interesting finding was that predicted NREI was negative for four of the eight simulations (Figure 2.4).

Simulations with regionally and temporally uniform drift density shows that regional differences in habitat characteristics did not contribute towards regional differences in predicted profitability (P_{∞}=0.13) (Figure 2.5, 2.6). In fact, predicted maximum NREI was nearly identical for the Snake and Sinuk which were the smallest and largest streams in my study with average discharge of 7 and 25 m^3/s, respectively. This shows that regional differences in drift density and size composition (Table 2.1) were responsible for the predicted regional differences in profitability (Figure 2.5, 2.6).

Discussion

My results support the hypothesis that opportunities for drift-feeding are better in Western Alaska than in Interior Alaska (Figure 2.3, 2.4). This finding may, in part, explain why Arctic grayling grow more rapidly and to a larger size in Western Alaska. These regional differences in foraging opportunity are the result of higher drift densities and larger invertebrates in Western Alaska (Table 2.1). Regional differences in the physical characteristics of feeding habitats do not contribute to the predicted regional differences in profitability (Figures 2.5, 2.6).

Regional differences in drift density and invertebrate size may be the result of relatively high salmon escapements in Western Alaskan rivers. This creates a trophic cascade, resulting in higher primary productivity and higher densities or larger benthic invertebrates (Bilby 1996; Wipfli et al. 1999; Chaloner et al. 2002). Direct consumption of salmon by invertebrates may also increase invertebrate biomass (Chaloner et al. 2004).

The effect of high resource abundance on fish growth in Western Alaska is likely to be magnified by low fish densities. This will boost per-capita resource abundance relative to Interior streams, particularly for fish smaller than 300 mm (Chapter 1). Western Alaskan streams also appear to be slightly warmer than Interior streams (Neyme, University of Alaska Fairbanks, unpublished) and combined with higher per-capita resource abundance this may contribute towards the higher growth rate of Western fish. This positive association between temperature and growth of adult fish is opposite to the one reported by Deegan et al. (1999) in their study of the within-stream effects of temperature on growth. This probably reflects the likelihood that they were working on a resource-poor stream.

Interestingly, depth and velocity were not important in explaining regional differences in foraging opportunity, and, in fact, there was no predicted difference between the largest and the smallest streams in the study (Figures 2.5, 2.6). This probably reflects the fact that all my study streams were large enough to provide foraging positions with optimal combinations of depth and velocity. This suggests

that the increase in growth rate associated with high flow, described by Deegan et al. (1999), was probably a consequence of a change in temperature or drift density rather than depth or velocity.

It is possible that life-history evolution has also contributed to regional differences in growth rate and maximum body size. The evolution of higher growth rates is to be expected when predation rates on small fish are high and opportunities for growth are sufficient to allow them to outgrow their predators (Chase 1999). Evidence suggests that early life-history predation mortality is much higher in Western Alaska, and, together with higher food availability, this may have favored the evolution of higher growth rates.

Most studies of habitat quality for drift-feeding fish focus on physical habitat characteristics, such as water depth and velocity, and devote little or no attention to invertebrate drift. This study suggests that it may be worthwhile to devote more attention to invertebrate drift in the future. However, while the model was able to explain regional differences in growth and maximum body size it limited our assessment of regional differences in food availability to sub-surface drift. A fuller assessment of regional differences in growth opportunities would also require information on the availability of other important food resources. These are known to include: shrews, sculpins, benthic invertebrates, salmon eggs, salmon carcasses, and salmon smolts (J.L. Neyme, University of Alaska Fairbanks, unpublished; A.L. DeCicco, ADF&G, personal communication). The

abundance of these resources is difficult to measure with existing techniques and new approaches that supplement the foraging model that I used would be useful.

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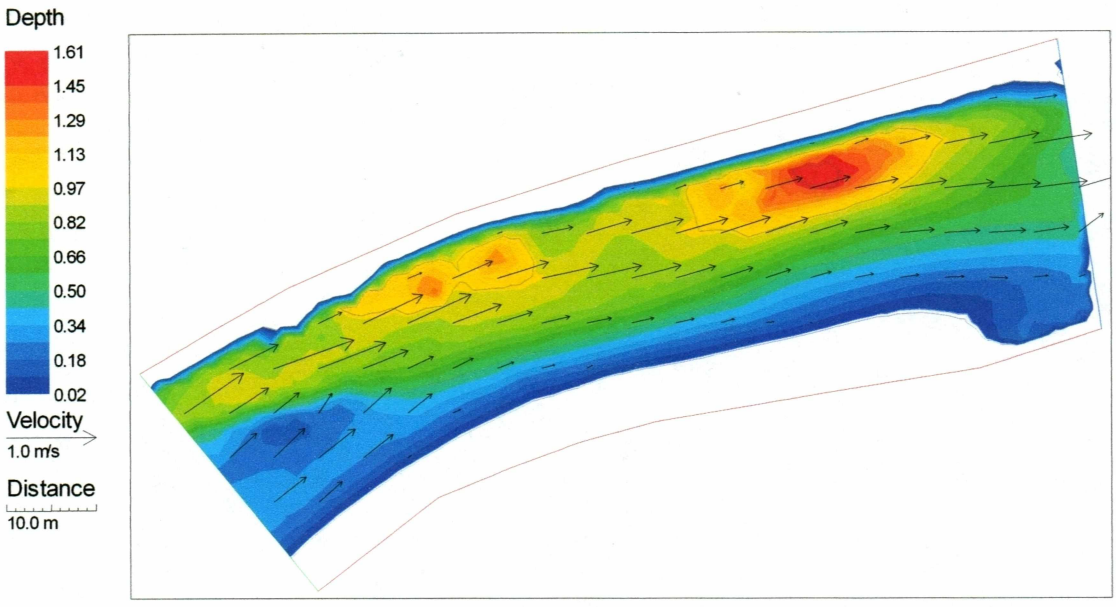

Figure 2.1-Example of depth contours with velocity vector arrows for the upstream pool in the Snake River.

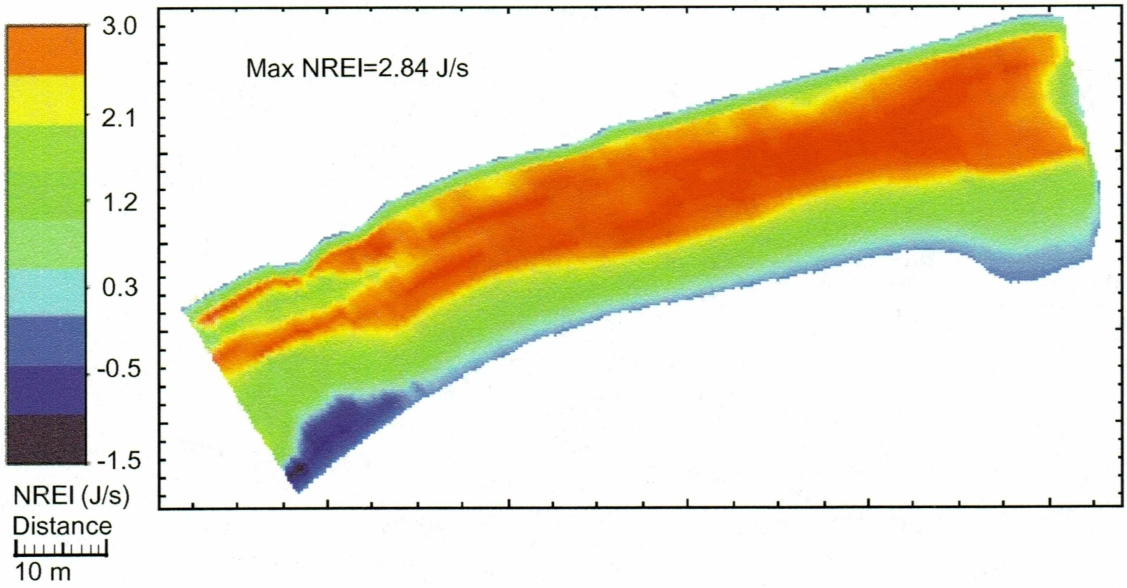

Figure 2.2-Predicted value of net rate of energy intake (NREI) for the upstream pool on the Snake River with predicted maximum NREI.

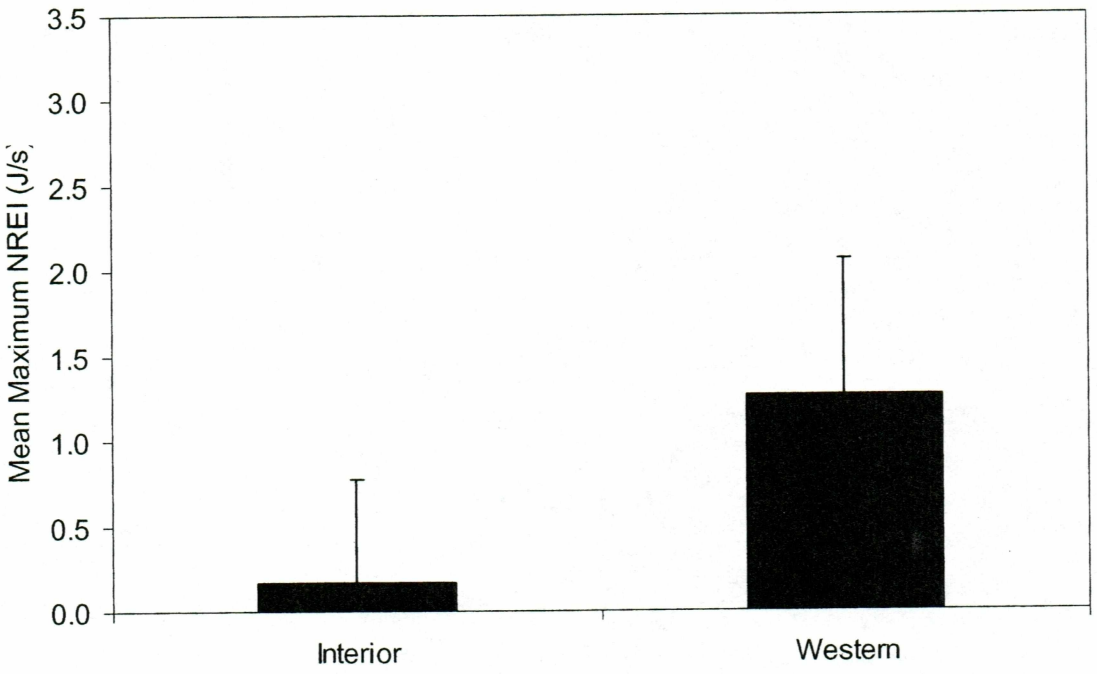

Figure 2.3-Comparison of regional mean maximum net rate of energy intake (NREI) and 95% CIs.

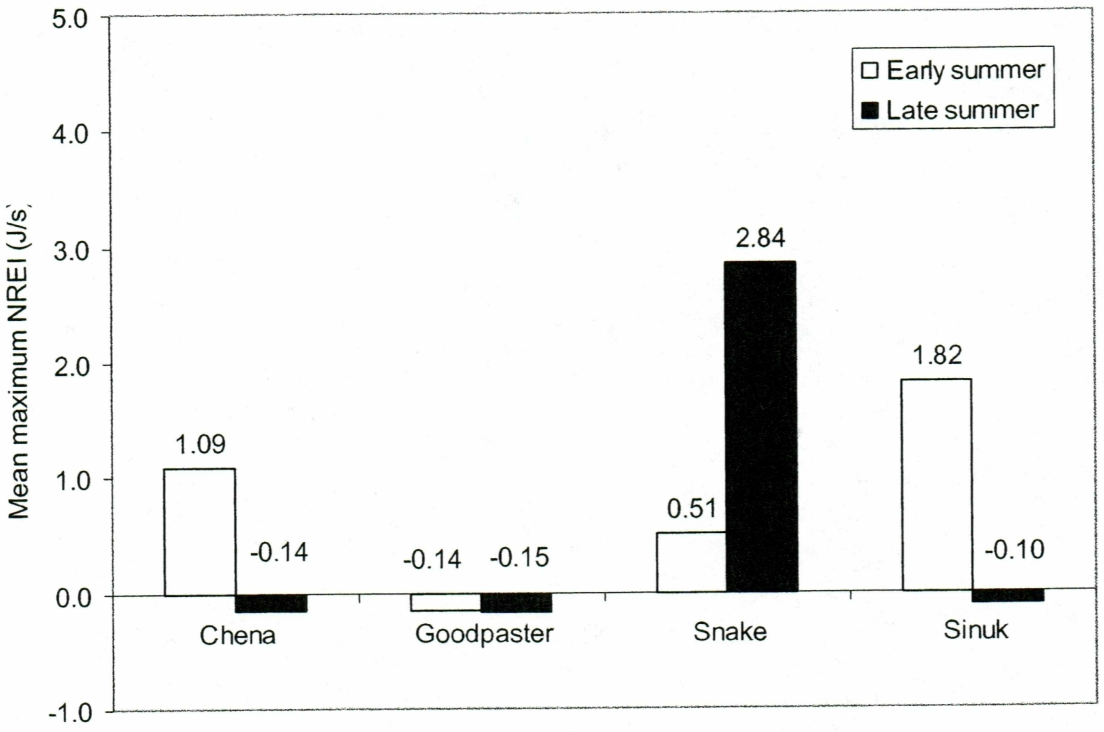

Figure 2.4 -Comparison of mean stream maximum net rate of energy intake (NREI) and 95% CIs.

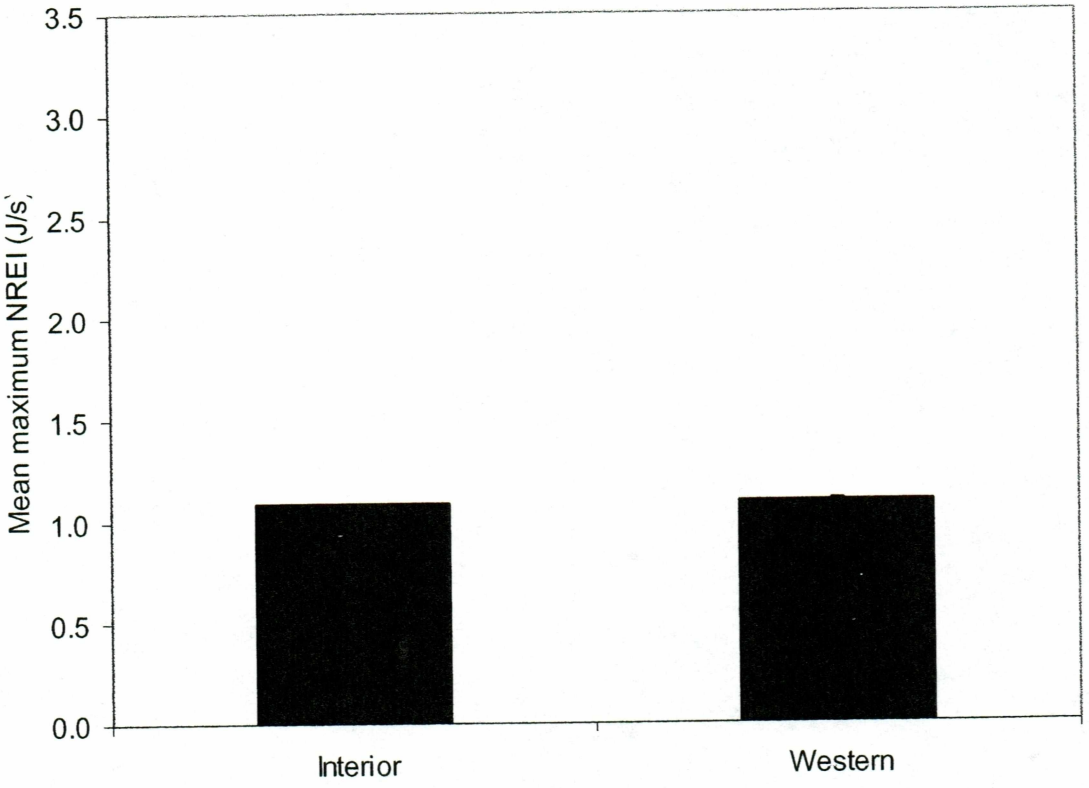

Figure 2.5 -Comparison of regional mean maximum net rate of energy intake (NREI) with uniform drift density and 95% CIs.

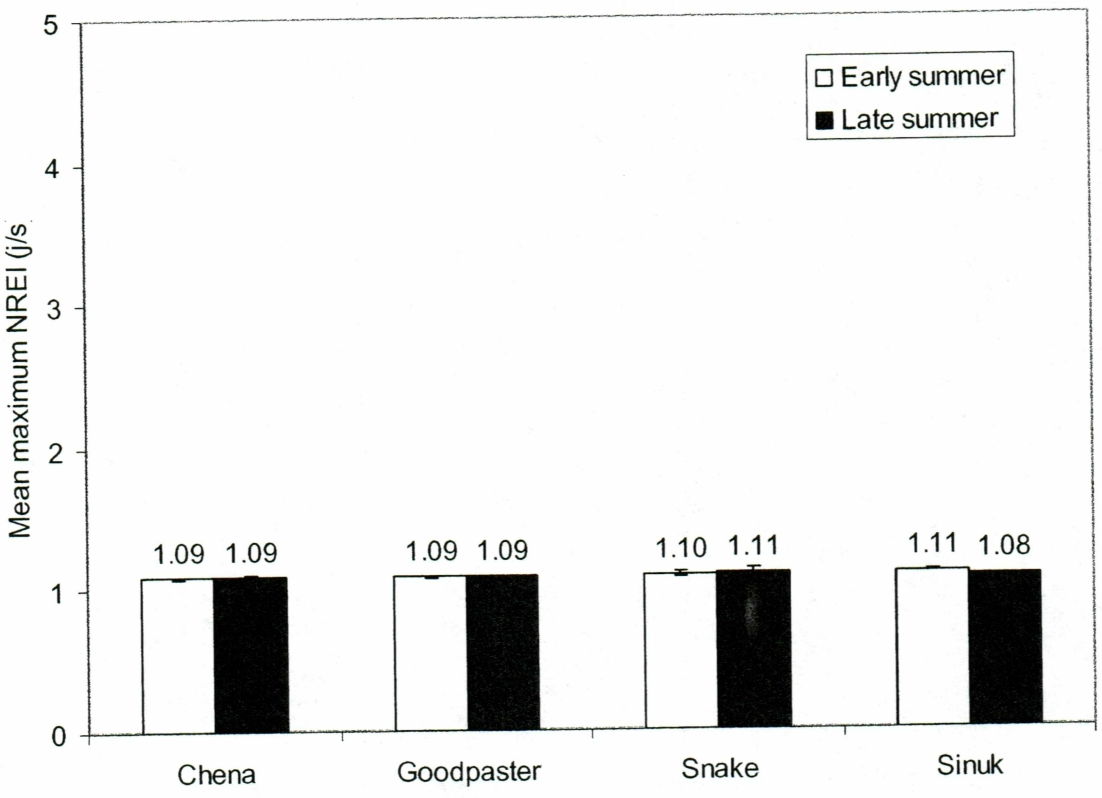

Figure 2.6-Comparison of mean stream maximum net rate of energy intake (NREI) with uniform drift density and 95% CIs.

Table 2.1- Invertebrate drift density (# of invertebrates/m^2) and dry mass (g) for each length category used in drift modeling simulations.

River	Sample period	Length (mm)	1	3	5	7	9	11	13
Chena	Early	Density (#)	0.10	1.14	0.72	0.12	0.02	0.02	0.00
		Weight (g)	0.01	0.12	0.43	0.20	0.05	0.08	0.00
	Late	Density (#)	0.03	0.02	0.06	0.01	0.00	0.00	0.00
		Weight (g)	0.01	0.00	0.02	0.01	0.01	0.01	0.00
Goodpaster	Early	Density (#)	0.64	0.49	0.06	0.01	0.00	0.00	0.00
		Weight (g)	0.08	0.06	0.02	0.01	0.00	0.00	0.00
	Late	Density (#)	0.20	0.08	0.08	0.01	0.00	0.00	0.00
		Weight (g)	0.04	0.02	0.08	0.02	0.00	0.00	0.00
Snake	Early	Density (#)	0.12	0.67	0.73	0.10	0.00	0.00	0.00
		Weight (g)	0.03	0.06	0.25	0.11	0.02	0.01	0.00
	Late	Density (#)	0.57	0.72	1.87	0.03	0.01	0.00	0.00
		Weight (g)	0.19	0.08	0.54	0.04	0.03	0.00	0.01
Sinuk	Early	Density (#)	0.19	2.29	1.20	0.23	0.04	0.01	0.00
		Weight (g)	0.06	0.19	0.37	0.20	0.08	0.01	0.00
	Late	Density (#)	0.53	0.52	0.08	0.00	0.01	0.00	0.00
		Weight (g)	0.13	0.04	0.05	0.00	0.02	0.02	0.00

GENERAL CONCLUSIONS

Summary

1. Chapter 1 shows that there are distinct regional differences in life-history and population dynamics of Arctic grayling. These regional differences in patterns of growth, mortality, and recruitment explain regional differences in the size structure of Western and Interior populations. Fish in Western Alaska grow more quickly throughout life and reach a larger maximum body size. Western populations are composed almost entirely of large (>300 mm), mature fish. In contrast, most fish in Interior populations are smaller than 300 mm.

While, no marked regional difference was found in the relationship between body size and the reproductive effort of spawning females or the relationship between body size and fecundity or egg size, the higher growth rate of Western fish means they probably allocate a smaller proportion of their annual energy budget to reproduction. However, these estimates of energy allocation are complicated by the possibility that fish do not spawn annually.

Mortality rates of mature Western fish are much lower than for Interior fish, but juvenile mortality rates are, correspondingly, higher. These regional differences are balanced by the lower recruitment rate of mature fish in Western populations.

Previous work on other species (Reznick and Endler 1982; Hutchings 1993) suggests that regional differences in Arctic grayling life-history could be the result of high predation rates, possibly by Dolly Varden, on small fish in Western

Alaska, or high predation rates on large fish in the Interior. It is also possible that the greater food abundance and warmer temperatures in Western Alaska combine to produce the fast growth and large size of Western fish.

2. Chapter 2 shows that the potential for drift-feeding is higher in Western Alaska than in Interior Alaska. The higher predicted maximum NREI's in Western Alaska were due to higher invertebrate drift densities and larger invertebrates, not the physical characteristics of the feeding habitat. These differences in size composition and density of the drift may have been the result of a trophic cascade produced by relatively high salmon escapements in Western Alaskan Rivers. Higher salmon abundance may result in higher primary productivity and higher densities of larger benthic invertebrates. Depth and velocity were not important in explaining regional differences in foraging opportunity.

While the model was able to explain regional differences in growth and maximum body size it limited our assessment of regional differences in food availability to subsurface drift. A fuller assessment of regional differences in growth opportunities would also require information on the availability of other important food resources.

Management Implications

1. The dramatic regional differences in life-history and population dynamics that I describe in Chapter 1 mean that Western and Interior populations will respond very differently to exploitation. In particular, the much lower recruitment rates in Western populations means they could be more sensitive to

harvest. It is also possible that recruitment in Western populations is under predator control, not the consequence of density-dependent competition early in the life-history. If so, then a reduction in the abundance of adults, as a consequence of harvest, is unlikely to increase the number of recruits-per-spawner and the population will not be resilient to harvest. In this situation harvest will decrease the abundance of fish and reduce recruitment, but there will be little change in the size-structure of the population.

In comparison to Western populations, Interior populations will be more resilient to harvest. This is a consequence of higher recruitment rates and also the likelihood that recruitment is probably regulated by density-dependent processes acting early in the life-history. In these circumstances harvest is likely to reduce competition amongst small fish and this will provide some resilience to harvest. In this situation, harvest will reduce both abundance and mean size of fish in the population, and, up to a point, increase recruitment rates.

This interpretation suggests it may be possible to use estimates of population size and adult mortality rate to develop ways to interpret harvest statistics. Populations in Western Alaska are much smaller than in the Interior and total adult recruitment is much lower, so, for these populations, a small harvest would be equivalent to a much larger harvest from an Interior population.

If, as I suggest, Dolly Varden predation in Western streams contributes to regional differences in life-history and population dynamics than there is an

obvious link between harvest management for Dolly Varden and population dynamics of Arctic grayling.

2. Western Alaskan Arctic grayling are prized by sport fisherman for their large size. In Chapter 2, I show that regional differences in food abundance probably contribute to the rapid growth and large size of these fish. For a manager this focuses attention on the factors responsible for the high per-capita food abundance in Western streams. These include high salmon escapements and the maintenance of clean waters and silt free stream gravel, which provide food and habitat for stream invertebrates and also food, overwintering, and spawning habitat for Arctic grayling.

It is also possible that lower fish densities contribute to the large body size of Western fish. If so, then any dramatic increase in population size is likely to reduce growth and maximum size.

Recommendations for Future Research

During the preparation of this manuscript new knowledge was gained, however, many additional questions about Arctic grayling were also raised.

1. More information is needed on juvenile Arctic grayling in Western and Interior Alaska including: growth and mortality schedules.

2. We need to better understand reproductive investment by Arctic grayling. We need a better understanding of energetic and reproductive costs and trade-offs associated with intermittent spawning.

3. We need to learn more about the role of salmon inputs, both direct and indirect, on the growth of Arctic grayling and other resident species.

4. We need to look at prey sources other than invertebrate drift and find new methods of collecting information on the abundance of these. We also need to develop better models to predict the contribution of these prey to the fish's diet.

LITERATURE CITED

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